A CRITIQUE ON PROFESSOR HAROLD HEATH'S CHIORÆRA DALLI, WITH SPECIAL REFERENCE TO THE USE OF THE FOOT IN THE NUDIBRANCHIATE MOLLUSK, MELIBE LEONINA GOULD.

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(From the Zoological Laboratory, University of Illinois, with Plates II to V.)

The remarkable Nudibranch *Melibe leonina* Gould has recently been described by Professor Chas. H. O'Donoghue, from the Vancouver Island region, under the nomenclature of Gould (1852), the discoverer of the species. Heath (1917) also employs Gould's nomenclature for the genus, but he goes farther than O'Donoghue by naming for it a new species, *Chioræra dalli*. Heath's species was collected off the coast of British Columbia. That is, not far from O'Donoghue's territory, nor, indeed, from that of Gould. The specific description of Heath, as far as it goes, coincides perfectly with that of Gould (1852), Cooper (1863), Fewkes (1889), Bergh (1904), O'Donoghue (1921) and Agersborg (1916, 1919, 1921, 1921*a*, 1922). The only difference lies in his statements in regard to the salivary glands and the tentacles. Microscopic sections of the anterior end of the alimentary canal of Heath's species no doubt will reveal these glands just as in the case of the type species of Gould. These glands, as I have shown before (1922), are very small, and are imbedded in the connective and muscular tissues of the neck, opening into the alimentary tract by minute crypts through the entoderm between the proventriculus and the mouth. Heath does not seem to appreciate Gould's description neither in the Latin nor in the English. It is, therefore, no wonder that Heath makes a new species of Gould's *Melibe leonina*.

Gould's description reads:

"Body limaciform, smooth and of a pearly and whitish colour, finely reticulate with orange. The head is enormously enlarged, with a distinct neck, semiglobose, the oral face flattened. The oral fissure is longitudinal, the lips large, with the true mouth within at the posterior portion; around the edge of the oral disc or cowl is a double series of orange-coloured cirrhi,

each of which has an independent motion. On the top of the head are two foliate expansions, destitute of venations, which answer to the true tentacles; on their anterior edge is an opaque whitish papilla, presenting something of a spiral or lamellar structure; they were sometimes wholly retracted within a permanent sheath." P. 310.

Heath's description reads in part:

"*External Features.*—The body (Pl. XI, fig. 1) comprises two distinct divisions, the head and the body proper. The head presents the appearance of a low vault or cowl provided with two dorsal tentacles, two sets of marginal tentacles and on its under surface bears the mouth. Unlike *Chioræra leonina*, the dorsal tentacles are not retractile, and in preserved material are plain, muscular, foliaceous outgrowth. Gould states that the tentacles of *C. leonina* bear on their anterior margins 'an opaque, whitish papilla, presenting something of a spiral or lamellar structure.' Nothing of the kind has been found to exist in the present species.

"The marginal head tentacles form two series, an outer set comprising from fifty to seventy-five large, slender processes, and an inner fringe formed of much smaller outgrowths of approximately double the number. Each of these cirri is provided with a nerve (Pl. XI, fig. 2) and gives evidence of being a tactile organ, though observations along this line were very incomplete.

"The mouth presents the appearance of a longitudinal slit (Pl. XI, fig. 1) placed near the posterior margin of the head, and therefore in close proximity to the anterior margin of the foot. Its posterior border may be said to be formed by the free border of the head, which here forms a deep angle usually devoid of the larger type of tentacle." P. 138.

"*Chioræra dalli* new species.

"Body limaciform, smooth and of a pearly color without definite signs of pigmentation. Head enormously developed, with the mouth near the posterior margin. Dorsal tentacles simple leaf-like expansions without special sheath. Jaws, Radula, and salivary glands wanting." P. 147.

From the above, it is seen the two descriptions agree exactly. The differences which Heath tries to bring out, are based on his failure to understand Gould's description, and also, judging from his own statement, he evidently made very superficial observations of the living animals. In preserved specimens, the whitish papilla is always retracted within a permanent

sheath; it is very hard to see in preserved specimens. In living animals, it seems to be very sensitive, although not so sensitive as the oral cirrhi, and, at the least disturbance, it is quickly withdrawn within the tentacular sheath, or stalk. Heath confuses the tentacular papilla, that is the true tentacle, with the foliaceous tentacular stalk. The tentacular stalk is never retracted. And, it was neither claimed by Gould. When this last named author writes: "*Tentaculae cephalicae foliatae, retractiles;*" he means exactly what he says on the same in English: On the top of the head are two foliate expansions, . . . ; on their anterior edge is an opaque, whitish papilla, presenting something of a spiral or lamellar structure; they were sometimes wholly retracted within a permanent sheath." It is clearly indicated by Gould's description that when he speaks of tentacles he includes the opaque, whitish, foliate papillae (one on each tentacle). That is, his "tentacle" stands for a whole; a part of a whole may be retracted within a whole, but the whole may not be retracted within a part of itself. The papilla stands for a part of the tentacle; the tentacle consists of the papilla and the foliate expansion. And, as I have stated above, the true, or real sensory organ, as far as the tentacle is concerned, is the papilla, which, *ipso facto*, is the actual tentacle, or the "rhinophore" of many writers, (*vide*: Agersborg, 1922). The rest of the tentacle, that is, the foliate expansions, is the tentacular sheath. It is only fair to Heath, to state here that the *papilla*, at times, may fall off from the stalk, since it is quite constricted at its base (Figs. 4, 5), but in a large number of specimens as examined by Heath, this should not be the general case. If an entire tentacle is stained in borax carmine, the papilla — completely retracted within the foliate expansion—will stain more deeply than the remainder. This is illustrated in Pl. IV, figure 6. In specimens preserved in alcohol or formaldehyde, the papilla may be overlooked easily. In point of fact, O'Donoghue (1921) claims no "rhinophores," p. 192, for *Chiorœra leonina*. This shows that the "papilla" is quite difficult to see. On page 193 he writes: "No structures comparable with the rhinophores of other nudibranches could be found unless the cephalic appen-

dages are their modified representative, which hardly seem probable." This, of course, is an error, and represents a good proof that the living animals, also in this case, were not studied carefully. As stated above, the sensory part of the tentacles is always retracted when the animal is disturbed, and may only be seen when the animal is left at rest in the aquarium. Then, it may become quite conspicuous (Pl. IV fig. 5*a*, *pa.*). O'Donoghue's statement, therefore, in regard to the absence of "rhinophores," indirectly substantiates my claims that Heath is wrong. With these things in mind, it is perfectly evident that Heath's description, as far as quoted, is a duplicate of Gould's. The rest of Heath's paper, as far as accuracy goes, is very similar to the part thus far reviewed. It is not my purpose to go into details here. I only wish to point out some of the main features. Heath's drawings are exceedingly unreliable as they are too diagrammatic (Fig. 6) and do not tally with his text. It is much to be regretted that Heath did not consult the literature. That would have saved him from creating a new species. In this case, there is no new species at all! (*Vide* literature on Nudibranches in general, and *Tethymelibidae* in particular: Agersborg 1916, 1919, 1921, 1921*a*, 1922). As regards Heath's drawings, it is only necessary to refer to his drawing of the tentacles which are represented by a *mere line!* Since the tentacles form one of Heath's basic reasons for creating a new species out of Gould's *Melibe leonina*, they should have been represented by very accurate drawings. That Heath's drawings of the tentacles are both incomplete and inaccurate, are supported by examination of preserved specimens from the vicinity of Heath's type locality. The structural features, as pointed out by Heath, in which his *Chioræra dalli* differs from Gould's *Melibe leonina*, are altogether too trivial, and his drawings too poor (Fig. 6), that I do not think anyone who knows Gould's species can possibly accept the species of Heath. The status of the genus itself is for the first time, to my knowledge, properly set forth by myself (Agersborg, 1921*a*). In this paper, the reasons are given why Gould's *Chioræra* is a synonym of *Melibe* Rang (1829). Several authors, moreover, although without giving a reason, recognize *Chioræra* as a synonym of *Melibe*.

(*Vide*: Tryon, Jr. 1883, p. 382; Fischer 1887, pp. 533–534; Bergh 1892, pp. 1039–1043; 1904, p. 13; 1907–1908, pp. 95–98). O'Donoghue (1921) although he classified *Melibe* under the nomenclature of Gould, states later in a letter to me: "I have quite given up *Chioræra* as a name." This, I am sure, will be the conclusion of every student who studies this subject seriously. In creating a new species, I think, Heath violated good usage among investigators by not familiarizing himself with the literature on the subject with which he dealt.

The species *Melibe leonina* Gould was quite fully described by me in an unpublished Master's thesis (1916), which is in the Library of the University of Washington, Seattle. It is not expected that Heath should know anything about this, but it goes without saying, that students of Zoölogy, nowadays, must consult the literature when they write for publications, lest their contributions to the science may be little less than a stumbling block for subsequent workers.

Heath's record of the swimming habit coincides with Gould's, also with mine (1916, 1919, 1921, 1921*a*, 1922, 1922*a*, 1922*b*). His description of the contents of the stomach and intestines differ. In my specimens, the alimentary tract contained crustaceans of various kinds, and of different sizes (Pl. V, figs. 7, 8, cr.). The food of *Melibe leonina* is crustaceous *per se*. (*vide litteraturae supra et infra*). *Melibe*, however, as I have pointed out elsewhere (1922*b*), is not such an able swimmer as *e. g.*, *Dendronotus giganteus* O'Donoghue.

Heath's reference to egg-bodies or nidosomes by the statement: "Large numbers of eggs were found attached to 'eel grass' and imbedded in gelatinous, spirally-wound folds after the fashion of many nudibranchs," does not agree at all with the nidosome of the Puget Sound species (Pl. II, fig. 2), whose egg-body (*vide:* Agersborg, 1916, 1919, 1921) consists of a broad ribbon (*not* "spirally-wound folds") which folds into a funnel-shaped form when supported in the water owing to one side of the ribbon being shorter than the other, and the shorter side becomes attached to the eel-grass. Heath's "spirally-wound folds" fit better to the nidosome of the "Sea-lemon," *Anisodoris* Bergh (*Anisodoris nobilis* MacFarland), (Pl. II,

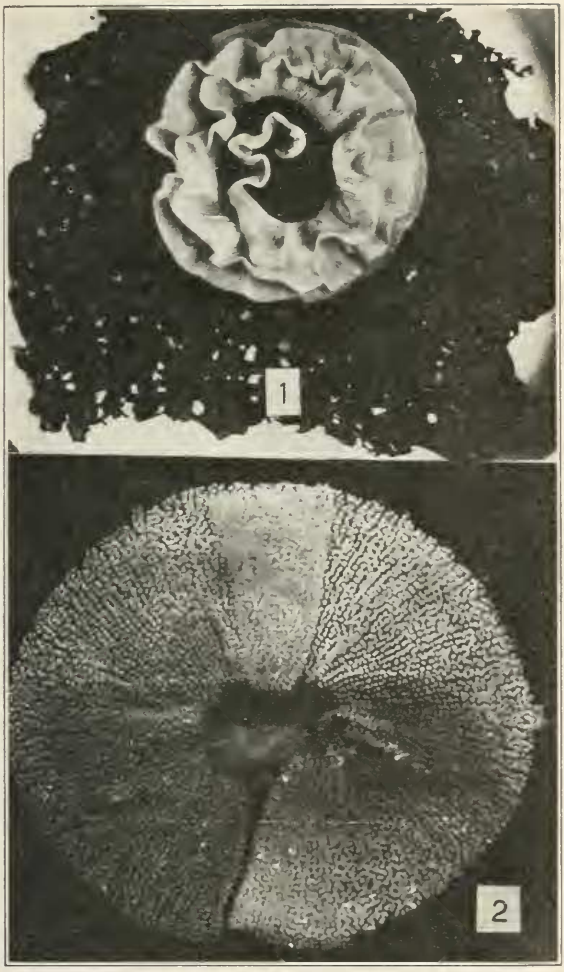

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Fig. 1. Nidosome of *Anisodoris nobilis* deposited on sea-lettuce (*Ulva lactuca*). Photo. by Dr. Sidney E. Johnson.

Fig. 2. Nidosome of *Melibe leonina* deposited on *Zostera marina*. Photo by author.

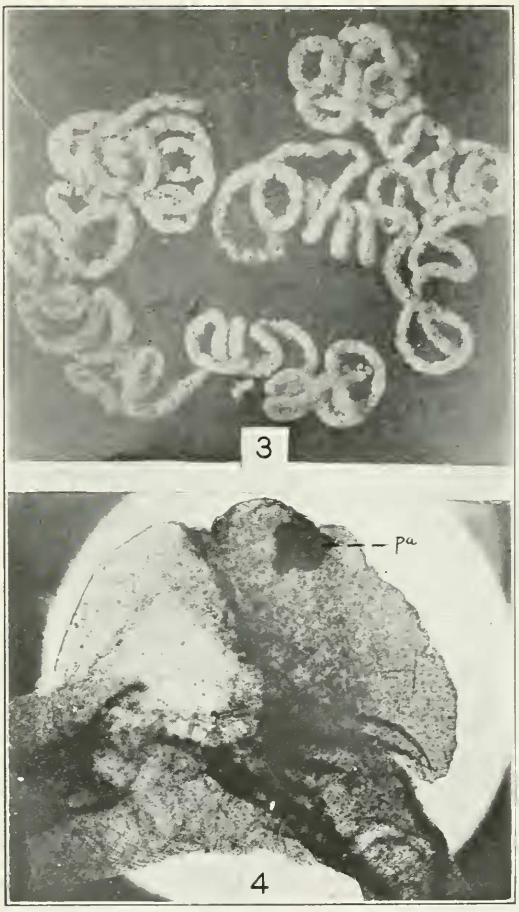

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Fig. 3. Nidosome of *Dendronotus giganteus*. Photo. by author.

Fig. 4. Dorsal tentacle from preserved specimen of *Melibe leonina* showing contracted papilla (*pa*) of Gould, stained with borax carmine, mounted in canada balsam. Photo. by author.

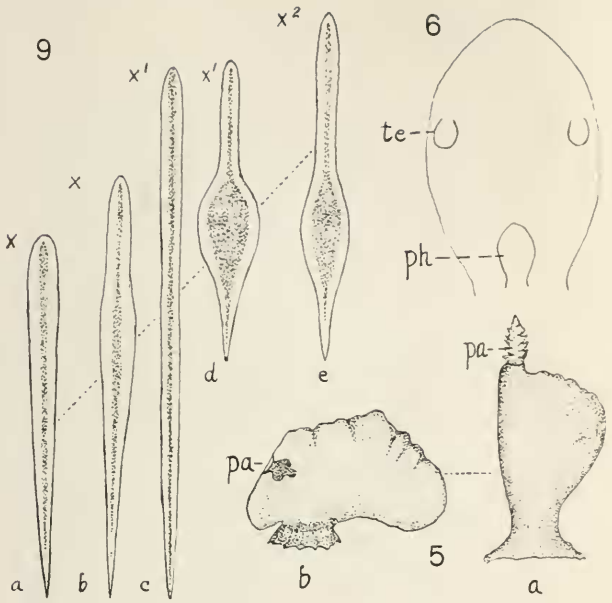

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Fig. 5 a. Drawing of dorsal tentacle of *M. leonina* from life, showing the papilla (*pa*) of Gould. b. The same from preserved specimen, seen with the unaided eye.

Fig. 6. Copy of Heath's drawing (pl. 12, f. 6) of the hood of "*Chiorxera dalli*", (= *Melibe leonina*). *te*, tentacle (dorsal tentacle). *ph*. pharynx.

Fig. 9. Diagrams illustrating various aspects of the foot of *M. leonina* during "galloping". *a*, normal; *b*, beginning (x) of elongation of the foot: *c*, maximum elongation, *x* advanced to x^1; *d*, x^1 adheres to substrate, large monotaxic pedal wave passes from anterior to posterior, and posterior end of foot is drawn anteriorly producing at the same time a large swelling on the middle of the body and foot. *e*, second elongation, a new wave sets in from anterior to posterior, repeating the same phenomenon as in *b*, x.

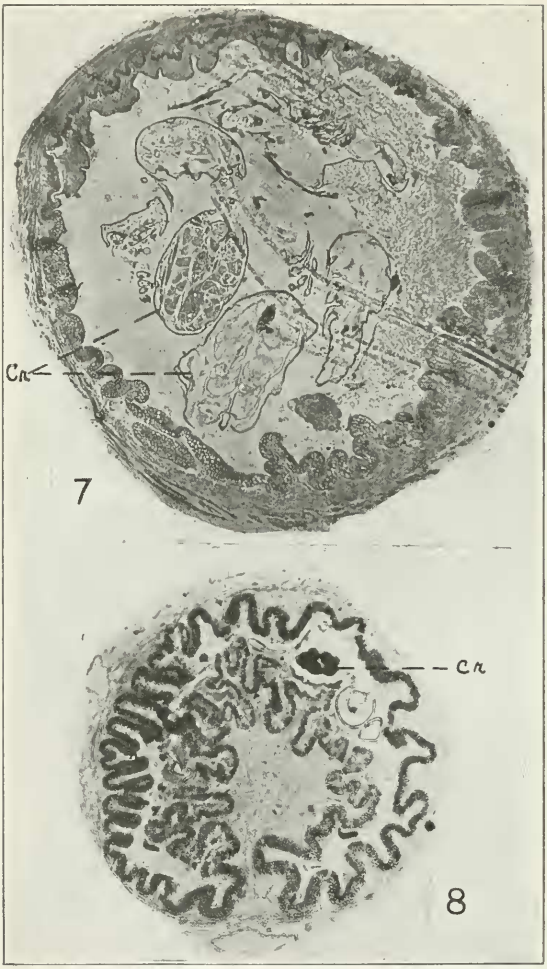

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Fig. 7. Microphotograph of a cross-section of the gizzard of *Melibe leonina*; *cr*, sections of crustaceans filling the stomach.

Fig. 8. Microphotograph of the cross-section of the intestine. *cr*., egg-pouches with embryos of crustaceans.

fig. 1). There can be no doubt as to the nature of the nidosome of *Melibe leonina*, as this species deposited two nidosomes in the laboratory during the summer of 1914 (*vide:* Agersborg, 1916, 1919, 1921); these were used as a check for those found in nature at that time, *e. g.*, on the eel-grass (*Zostera marina*), where *Melibe* also were collected. The same kind of nidosomes had been found before by members of the Puget Sound Biological Station, but it was not known to what species it belonged until *Melibe leonina* was seen to deposit the same kind in the laboratory. Closely related species among the *Aeolidia* deposit nidosomes of great similarity: *Aeolidia coronata*, *Hermissenda opalescens*, *Coryphella longicaudata*, etc. (Fig. 3). The extent of the spiral form of a nidosome of this kind depends on two things: (1) on the speed of the egg-mucus flow, and (2) on the speed with which the nudibranch moves during oviposition (Agersborg, 1922*c*). In the light of these facts, I am compelled to doubt, therefore, very much whether Heath's statement in regard to the nidosome of his species is any more valid than his supposed new species. Of course, Heath's inference is only a guess. I have suggested above the only scientific way to identify nidosomes.

O'Donoghue (1921) makes the following statement in regard to *Melibe leonina:*

"There seems little doubt that this species is mainly pelagic for it is found floating freely in the sea during the early months of the year and I have seen it at the end of July and the middle of August. Towards the middle or end of May, however, it comes in to spawn and it is then very plentiful. . . . At this time, the animal is present in hundreds and so constitutes an extremely common form at these two points (on the Zostera beds at the Station and at Mudge Island). Even then, however, it does not creep about on the eel grass but only seems to adhere for the purpose of laying its eggs. In the laboratory too it does not creep on the sides of the aquaria and only rarely clings to them. It has not been observed creeping on anything after the manner of other Nudibranchs and if not entirely a pelagic form like *Phyllirhoe* it is beyond doubt very nearly so and is a most interesting form." P. 194.

Inability to use foot for the purpose of locomotion on the substratum as suggested by O'Donoghue does not hold. *Melibe leonina* though pelagic *at times* is quite able, as we will see, to use the foot in locomotion by the means of creeping. Professor Trevor Kincaid kindly informs me that in the summer of 1917 he found one of the bays of Hoods Canal literally filled with this species—there were an incredible number—"millions of them." The piles under the docks were covered with them.

(I am under the impression that Professor Kincaid also stated that *Melibe* was clinging to the piles above low-water mark at low tide; if this be the case, it is the first time on record that this species has been seen alive on dry land; it will be noted, that the body of *Melibe leonina* is so soft and watery that it loses very soon its fluid-contents when left out of water. This is at least true when the animal is lifted out of water and examined on a glass plate). From the same source, I have the corroboration on the point in regard to locomotion: *Melibe leonina* is perfectly able to creep on a solid substratum. I am very much indebted to Professor Kincaid for this point of information, not only because of the unusual nature, *e. g.*, as regards the occurrence of *Melibe* on the piles above low-water mark, and the great abundance in which it appeared; but also, for his statement in regard to the locomotion of *Melibe leonina*.

M. leonina, then, uses its foot for creeping purposes! As shown elsewhere, (Agersborg 1919, 1921, 1922, 1922b) the foot is highly ciliated, and the ciliated ectoderm is innervated with nerve fibres from the nerve-net which is spread throughout the foot. During the summer (1921) while working experimentally on the chemical sense of *M. leonina* (Agersborg 1922a). I had the opportunity to study this species very closely. As stated above, its food consists of small crustaceans of various kinds: copepods, isopods, amphipods, etc., judging from the contents of the alimentary tract (Pl. V, figs. 7. 8). In the laboratory, I fed it on *Caprella* and *Gammarus*, about 20 to 15 mm., long, respectively. The former, although it fastened its claws into the membrane of the mouth of *Melibe*, was nevertheless pushed down into the oesophagus, proventriculus, gizzard, etc. of *Melibe*. The latter was executed in the same way. I